Sex- and season-dependent behaviour in a þightless insect, the Auckland tree weta ( )

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resources essential to female survival and reproduc in a sexually dimorphic, harem-forming insect, the Auckland tree weta ( ). First we established artiýcial cavities as diurnal refuge cavities and potential harem guarding sites. We then examined cavity occupancy changes, and, based on our knowledge of prior occupants, determined sex-speciýc patterns of arrival, departure, and aggregation at a population level throughout the year. Both season and the sex of prior occupants inþuenced weta occupancy patterns. Most observations were of single females. However, both males and females moved into cavities previously occupied by a weta of the opposite sex more often than expected by chance alone. Females avoided cavities where other females were present, except during summer when most harems formed. In early summer, male and female tree weta previously living apart began co-habiting. Generally there was little relationship between the number and sex of the weta inside cavities and female

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female weta at this site are mobile and may search for mates during the summer. The data are consistent with a polygynandrous mating system as inferred for other tree weta species (spp.).

Keywords: aggregation; harem; mating system; Orthoptera; polygyny

Introduction

Searching for mates can be costly (Gwynne 1987; Acharya 1995), but nonetheless is a requirement for most sexually reproducing organisms (Kokko & Wong 2007). Search effort in one sex is dependent on search effort in the other (Hammerstein & Parker 1987), but because males may beneýt more from multiple mating than females (Bateman 1948) males are generally predicted to mate-search more than females when multiple mating is common and sperm competition occurs (Kokko & Wong 2007). However, males may attempt to monopolise resources, including females, if doing so increases reproductive success.

In a polygynous mating system, males compete directly for access to females through male ï male combat (cf. Darwin 1874) or indirectly by locating and defending sites with

rate with potential mates, they might be mom ɹ ᵠ א ƙ l ᴰ ᵀ Mof sneakers (or satellites), as well as residents, can favour mobile males (Reichard et al. 2004). Differences in aggregation and occupancy patterns between the sexes can thus occur both spatially and temporally as a consequence of both sex-speciýc searching patterns and mating system (Lehmann & Perrin 2003). Nonetheless, data that report seasonal changes in sex-speciýc searching and aggregation behaviour are predominantly from well-studied, large diurnal species. Data are still lacking for many taxa, and particularly for many insects.

In many Orthopterans, males call, using stridulatory

These characteristics suggest that tree weta movement patterns

smaller scale with one cavity and entrance on each side. Each artiýcial refuge thus had two unlinked, same-sized cavities, one with an entrance on the top left, and the other with an entrance on the bottom right. Cavity entrances were approximately 2 Ĭ 2 cm. Each cavity measured approximately 25 Ĭ 150 Ĭ 5 cm internally, providing space to accommodate approximately eight adult tree weta.

Refuges were established in April 2008 and monitored until August 2009. In the ýrst 28 days after attachment to trees, we recorded the number and sex of weta in each cavity daily, doing so without disturbing them while they were resting during the day. We amʹ d] ʹ

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(maximum: = 142 in March 2009), and the amount of cavities occupied reached 81% and 82% in March and June 2009. The mean number of weta per occupied cavity peaked in late summer (¯ = 4.5 weta per cavity, excluding empty cavities).

Weta aggregations

Most observations of single tree weta (= 1249) were of females (= 849). Single weta observations were double those of tree weta sharing a cavity (= 660). After single weta, maleïfemale pairs, one male with two females, and one male with three females were the next most common groupings. Throughout the year, the number of cavities that were previously vacant, occupied by one female, a pair, or a harem changed signiýcantly by visit (Friedman rank sum test p-value < 0.001; but p-value = 0.328 for cavities occupied by one male). Aggregation patterns changed dramatically after Day 221, at the end of spring (Fig. 2). Over the summer (days 250ï310) increasing numbers of male and female weta were observed together in cavities, in contrast to previous observations of single weta. Fewer single females were observed, with an increase in both pairs and harems (Fig. 2). The maximum number of females with a single male in one cavity was ýve, which we recorded on three occasions (in December, February and July respectively). To further explore the positive correlation of male and female numbers during the summer, we analysed male and female arrivals and departures in the cavities.

Male arrivals

Male occupation of cavities (Table 1) overall was non-random. During the initial colonisation period (Period A), no male-occupied cavities were occupied in the next observation period by two males (= 2160 total observations, = 63 male colonisation events; see Table 2). In the following winterïspring (Period B), only two male-occupied cavities were colonised by a second male and the male-avoids-male effect was strong (= 701 total observations, = 61 male colonisation events; see Table 2). This effect was insigniýcant (p > 0.05) in both summer and late autumn (Periods C and D). In contrast there is no evidence that male weta avoided cavities based on the

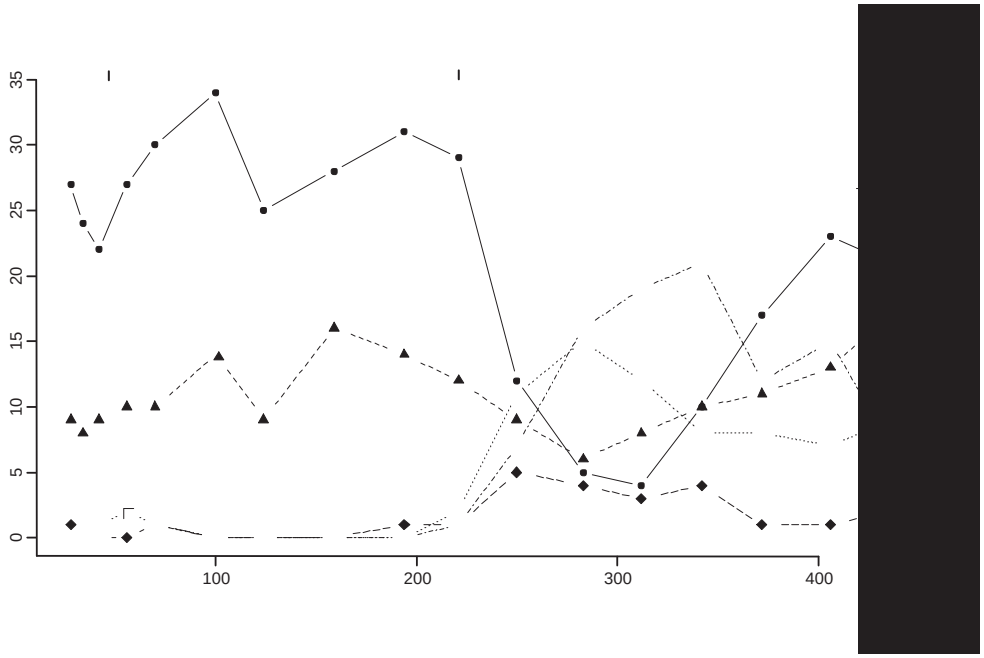

Table 1. Likelihood of occupancy in an artiýcial cavity by a new Auckland tree weta ( ) arrival is dependent on the previously recorded occupier of that cavity. An odds ratio of >1.00 indicates that a particular cavity type

Figure 5. Proportion of male and female subadult Auckland

in both time periods, and if the time periods are combined, the signiýcance of these results is strengthened (odds ratio = 0.232, p-value = 0.021 for males leaving harems and odds ratio = 7.29, p-value = 0.000 for males leaving other males). Otherwise, male departures were not signiýcantly different between different habitation types in summer or autumn ï winter. Analysis of Period C and Period D data shows no signiýcant patterns in female departures.

Sex ratio and age structure

There were more females than males in every daily and monthly count throughout the research period. The average ratio of females to males was 2.5:1 in the ýrst 28 days and 2.1:1 from May 2007 through to July 2008. The proportion of occupied cavities containing weta of both sexes changed markedly through the year (Fig. 4), but sex ratio did not. Few immature weta were present in artiýcial cavities during the ýrst few months of colonisation (3.9% of total in April, and 6.1% in June 2008; Fig. 5), but immature weta numbers increased in autumn 2009 (14ï 17% of total). Immature males outnumbered immature females.

Discussion

For the ýrst time, we show changes in tree weta aggregation and movement patterns associated with occupancy of diurnal refuge cavities through the seasons. A clear change in aggregation patterns was observed in early summer when increased numbers of male and female weta were recorded together in cavities. This contrasts with the high proportion of cavities with single weta observed in the previous winter and spring. The formation of harems appears to result both from female weta no longer avoiding other female weta and from males moving into cavities with one or more female weta. Our data show that males occupied cavities with a female present more often than either empty cavities or cavities with another male present, both during the initial colonisation and in the summer. This result is consistent with cavity choice experiments in (Kelly 2006c) where males search for mates, as might be expected in a polygynous species where sperm competition is likely occurring (Kokko & Wong 2007; Kelly 2008a). However, patterns of female occupancy also demonstrate that, throughout the year, females joined cavities more often than by chance where a prior male occupant had been recorded. If female movement patterns are associated with the search for mates, this suggests that females also make choices about prospective mates (Spencer 1995), and that co-habitation with males may not lead to the high costs that occur in (Kelly 2006c). Although female tree weta do not receive a nuptial gift, males might control access to the daytime refuge that is a resource requirement, and therefore contribute to female searching or movement patterns. The female arrival and departure patterns apparent here contrast with behaviour patterns recorded in that indicate females are more sedentary than males, but agree with ýndings that both females and males are mobile, and that polygynandry might be a better descriptor of the mating system than polygyny (Kelly 2006c).

We emphasise that we make no claims about the behaviour of individual or ótypicalô weta. Instead, we focus on changes in occupancy patterns, and our conclusions pertain to weta (plural) as a population rather than to individual weta. Thus, although the same individual weta might be using a cavity where occupant age and sex are unchanged between monthly observations (Spurr & Berben 2004; PMW unpubl. data), our results do not rely on this assumption. The data clearly demonstrate that changes in cavity occupancy numbers for males and females show signiýcant dependency on initial occupancy of the cavity. This leaves some uncertainty as to how the dependency works at the individual level; for example, occupancy change in a cavity between visits may not necessarily come about in the simplest possible way, such as through the arrival or departure of a single weta, although this may in fact be the case. Nonetheless, the existence of the effects themselves on the occupancy pattern of the population is evident.

The odds ratios for a female moving into a cavity occupied by one or more females (compared with a vacant cavity) suggest that female weta avoid other females for most of the year. However, in early summer, this pattern changed. Factors inþuencing female departure rates are not clear, but from our data it seems unlikely that males evict females after mating (cf. Kelly 2008b), as estimated male departure rate was similar to female departure rate (Table 2). During the summer most adult females were observed in harem groups, and about 64% of females recorded in one visit were present in that cavity in the next visit. Female eviction thus seems qting

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